BUOYANCY CONTROL AND SIPHUNCLE FUNCTION IN AMMONOIDS

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ABSTRACT. The question of buoyancy control of ammonoids in relation to the function of the siphuncle is analysed in the light of flotational experiments on exact models of moderately evolute and highly evolute shell types, and the structure of the siphuncle. It is demonstrated that, if the mode of life of the ammonoid animal were analogous to that of living *Nautilus*, the relatively more buoyant shell of most ammonoids would have needed considerably more liquid in its chambers than *Nautilus*, with many of the chambers completely filled. The structure of the siphuncle, and its location in the last chambers of the majority of coiled ammonoids, is such that it may have been non-functional in these chambers so that the animal did not vary the quantity of liquid in them. We believe that most ammonoids were fairly efficient at moving themselves vertically but less efficient as swimmers.

SPECULATION about the function of the chambered cephalopod shell has provided one of the more fruitful sources of research topics in palaeontology for more than a hundred years. Starting with Moseley's (1838) mathematical treatise, recently updated by Raup and Chamberlain (1967), numerous papers on the subject have appeared. A review of earlier work is given by Westermann (1971). However, as far as we are aware, the line of reasoning we use, and the data upon which it is founded, are new.

Apart from attempts at finding a purely mathematical solution for the problem (an attractive one because the shell approximates a logarithmic spiral), by determining the location of the centre of gravity and the volume of idealized and, of necessity, unornamented shells, there have been attempts to derive conclusions by a combination of deduction and direct observation on particular shell types. The most noteworthy of these trials was made by Trueman (1941). The conclusions drawn in this study have had a remarkably strong and persistent influence on workers in the field, despite the fact that some of his suppositions, such as the asserted positive correlation between the dimensions of the body chamber and those of the chambered portion of the test, are no longer possible to maintain (Reyment 1973).

Reyment (1958) made an experimental study of the post-mortal fate of chambered cephalopod shells. No attempts at reconstructing the mode of life of fossil cephalopods were made in this work, and all experiments were carried out on models of straight and coiled nautiloids, as well as the shells of two living species of *Nautilus*. In so far as the results of this work could be applied to buoyancy control interpretations of fossil chambered cephalopods, they did not suggest anything other than that the empty *Nautilus* shell can be brought into hydrostatic equilibrium with seawater by a slight increase in the load of the shell. The work of Bidder (1962) and Denton and Gilpin-Brown (1966) demonstrated that weight adjustments in the shell of *Nautilus*, for compensating for shifts in the hydrostatic conditions, are made by the secretion or transfer of relatively small quantities of liquid via the siphuncle into the final chambers. The last chamber is normally full or almost full of this liquid and earlier chambers contain progressively less and less of it. The majority of the chambers are gas-filled and empty of liquid.

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Until we compared notes on our recent research on the ammonoid shell, there did not seem to be any reason to doubt that the ammonite animal functioned in the same way as the living *Nautilus*, both with respect to the operation of the siphuncular mechanism and to the approximate number of chambers containing cameral liquid. The results of our studies, Mutvei on the structure and interpretation of the ammonoid siphuncle, and Reyment on the post-mortal properties of ammonoid shells based on experiments on models, have shown that the currently accepted interpretation of the hydrostatic behaviour of the ammonoid shell cannot be sustained without modification and clarification.

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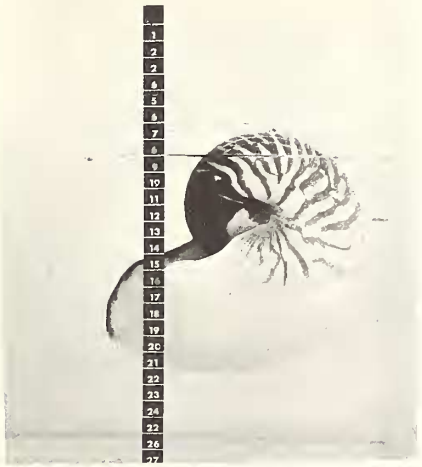
BUOYANCY OF EMPTY AMMONOID SHELLS

There are two approaches open for the study of the buoyancy of empty ammonoid shells. One is by means of accurately constructed models of shells. The other is by calculations of the buoyancy properties of various kinds of shells, the basic assumption being that the growth of the shells has taken place in accordance with the logarithmic spiral.

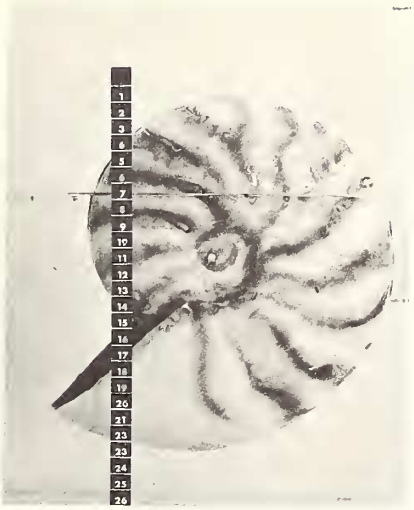
The second approach has an appeal in this day of the computer, but it has the obvious limitation that it can only give an indication of the floating orientation of a particular shell type. At the present stage of its development, it cannot be used to find the proportion of the empty shell that floats above water, nor is it suited for investigations of the critical sinking loads of particular shell types.

Study by accurately constructed models of key morphological types is the only really satisfactory means of testing hypotheses on the relative buoyancy properties of chambered shells and their application to palaeoecological reconstructions. However, such models are expensive to make, requiring the assistance of a highly skilled technician with an ability to sculpture, and suitable specimens upon which to base the models are hard to come by. A detailed account of the way in which our models were built is being presented elsewhere (Reyment 1973). They were made from plastic by the method of vacuum-moulding so as to conform exactly to the structure of the actual ammonoid shells upon which they were based. The correct specific weight (Reyment 1958) was obtained by electroplating the model, internally and externally, with a suitable metal.

The shell categories here studied by this method are of the ceratitic type, being based on *Ceratites nodosus* (von Buch), *Discoceratites intermedius* (Philippi), and *Ceratites* (*Acanthoceratites*) *spinosus* Philippi, selected from the extensive collections in the Paleontologiska Institution. All three possess the same basic shell structure, namely, high whorls, moderately evolute coiling, and moderately strong ventrolateral tuberculation: they differ from each other only in the degree of inflation of the shell. Thus, the *Discoceratites* is sub-oxynote and the *Acanthoceratites* is sub-cadicone.



TEXT-FIG. 1. Floating position of *Nautilus pompilius*. Fresh shell obtained from the Solomon Islands. Scale in cm.



TEXT-FIG. 2. Floating position for model of *Discoceratites*. Scale in cm.

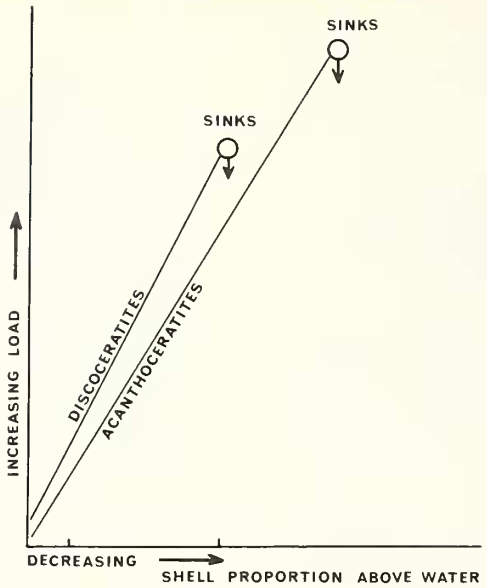
The important class of highly evolute shells was studied with models based on dactylioceratids. No particular species was used as basis for construction.

Flotational experiments. The weight increase required to cause the models of ceratitids to just attain the point of sinking was determined. This may be done in two ways: either by filling larger chambers with water, or by merely weighting the shell with lead shot in the body chamber. The former method is biologically more realistic, while the latter is more expedient and does not damage the models; it has the drawback that it is accompanied by an unrealistic displacement of the centre of gravity. Although the difference in loads yielded by the two procedures is slight (they cannot be the same because of the load to air volume ratios), the chamber-filling alternative was selected for the present work.

Firstly we draw attention to text-fig. 1, which illustrates the floating position of a fresh *Nautilus pompilius* from the Solomon Islands. This shell, which floats relatively low in the water, required no more than an increase of 13% in weight in order to sink.

Text-fig. 2 shows the floating position adopted by a model of *Discoceratites*. It floats very much higher in the water than the *Nautilus*, 27% of the shell being above water as compared with 10%. Approximate determinations of the buoyancy of the empty shells show that the ceratites require weight increases of from 35% to 45% in order to sink. They are, therefore, when empty about three times more buoyant than the *Nautilus*. Text-fig. 3 compares, schematically, the load-to-sinking-point relationships for *Discoceratites* and *Acanthoceratites*; this is linear as to be expected. As is also to be expected, the more depressed and spacious shell requires a greater load to make it sink than does the compressed shell.

Why these substantial differences between the nautiloid and the ammonoids? There



TEXT-FIG. 3. Load-to-sinking curve for the models of *Discoceratites* and *Acanthoceratites*.

are several reasons. Firstly, *N. pompilius* is highly involute and only the chambered part of the last whorl contributes to the uplift (Reyment 1958). The more evolute ceratites have a significantly greater chambered surface area available for uplift involving part of the inner whorls. Secondly, the ceratites have a greater relative cameral volume, owing to their higher whorl sections. Thirdly, ammonoids tend to contain relatively less shell substance for a given conch volume than nautiloids, owing to their mostly thinner walls: this is a well-known fact, most recently studied by Westermann (1971). Fourthly, the ammonites studied in the present connection have a smaller apical angle than the nautiloids, the body chamber does not 'flare' pronouncedly in the manner characteristic of *N. pompilius* and *N. scrobiculatus*, for example (cf. Reyment 1958, pl. 2). In consequence, the dead weight of the body chamber is less in the ammonoids studied than in the *Nautilus* species.

The differences between the buoyancies of the *Nautilus* shell and the ceratite models are so great that they exceed any reasonable limits of experimental error. It was ascertained experimentally that even with a construction error of 25% in the shell weight, the buoyancy differences are such as would require special explanation and interpretation.

Highly evolute shells. Two models of shells of dactylioceratid type were made. There were two categories considered in this part of the work: those with a body chamber occupying seven-eighths of a whorl, and those with a body chamber occupying one-and-a-third whorls.

The floating position taken up by the highly evolute shells was shown to be highly

TEXT-FIG. 4. Floating position for model of dactylioceroid shell with a body chamber length of one-and-one-third whorls. Scale in cm.

TEXT-FIG. 5. Floating position for model of dactylioceroid shell with a body chamber length of seven-eighths of a whorl. Scale in cm.

dependent on the length of the body chamber. The model shown in text-fig. 4 has the greater body chamber. It floats as low in the water as the *Nautilus* depicted in text-fig. 1. The liquid in the chambers of the living animal would not need to have occupied more than a few of the chambers. The model shown in text-fig. 5 has the smaller body chamber. In order for the ammonite to have been oriented vertically during life, numerous chambers would have had to have been permanently flooded.

IMPLICATIONS OF THE BUOYANCY EXCESS OF AMMONOID SHELLS

The relative buoyancy of the ammonoid shell becomes greater with increasingly evolute shells; this may in part be offset by an increase in the length of the body chamber. This is a logical outcome of the increase in 'effective volume' of the shell in relation to its weight. Thus, the more completely evolute the shell is, the greater is the uplift on it, and the lesser is the downward force due to the shell weight. If the ammonoid animal had the same mode of life as the living *Nautilus*, certain conclusions concerning the function of the hydrostatic mechanism of its shell are inescapable.

Empty ammonoid shells more evolute than *Nautilus*, with the same length of body chamber, must have floated considerably higher in the water. We note in passing that there is a differentiation within the species of living *Nautilus*; the slightly more evolute *N. scrobiculatus* floats higher out of the water than does *N. pompilius*, although there is a slight difference in the apical angles of the whorls of these shells (Reyment 1958).

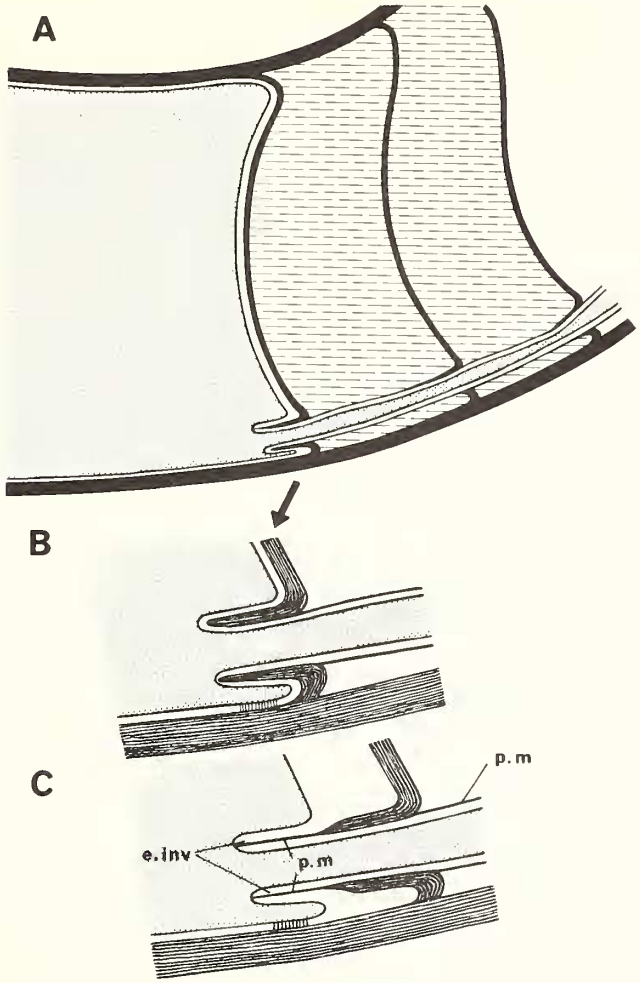
It is unfortunate that the surviving genus of chambered cephalopods comprises species whose shell morphologies are not typical of most members of the class, and in particular the ammonoid branch. In fact the atypical nature of the *Nautilus* shell, with its highly involute shape and large body chamber diameter, may be responsible for obscuring the probable function of the ammonoid shell for so long.

For shells of the ceratitid type, with high, subrectangular whorls and moderately evolute shape, more than half of the chambers of the last whorl, and probably all the lower chambers of the second last whorl, must have been entirely filled with cameral liquid if the shell functioned hydrostatically in the same manner as poised shells of living *Nautilus*. This has certain, albeit minor, consequences for the floating position adopted by the animal in life. Buoyancy adjustments must have been made in the chambers located in the uppermost third of the vertically poised shell, and at least in the last two to three whorls, depending on the nature of the coiling, and the amount of cameral liquid.

THE STRUCTURE AND INFERRED FUNCTION OF THE SIPHUNCLE

The structure of the wall of the siphonal tube. The position of the siphonal tube in most ammonoids tends to be constant. Except for the ontogenetically oldest part of the shell, it is situated close to the ventral (anatomically posterior, outer) side of the whorls. Its diameter is usually small. Characteristic for the majority of Mesozoic ammonoids, as well as several Palaeozoic ammonoids, is that the septal necks change their direction during the ontogenetic growth of the shell. Thus, in the early stages they are directed towards the shell apex; in the later stages they point towards the body chamber. On the basis of their direction, the septal necks are said to be retrosiphonate and prosiphonate, respectively.

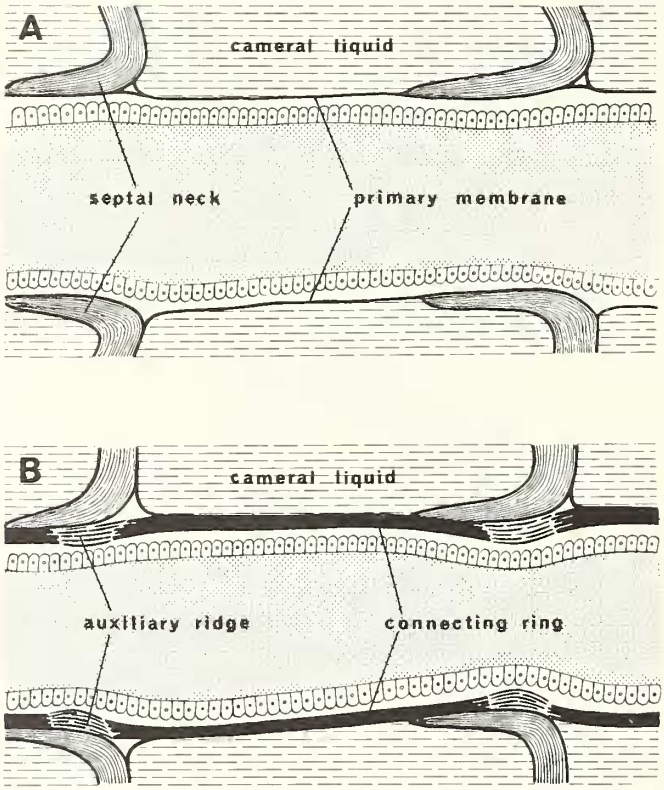
The direction of the septal necks is intimately related to the structure and origin of the connecting rings. In *Nautilus*, which has retrosiphonate septal necks, each connecting ring is composed of an outer spherulitic-prismatic layer and an inner conchiolin layer. The spherulitic-prismatic layer is a direct continuation of that layer in the outer part of the septal neck, whereas the conchiolin layer originates from the nacreous layer of the septal neck (Mutvei 1964*a*, 1972). On the other hand, the ammonoids with prosiphonate septal necks have connecting rings which seem to be composed solely of a conchiolin layer (Mutvei 1967; Erben and Reid 1971). The calcareous prisms and the carbonate fluorapatite in the connecting rings, reported by Birkelund and Hansen (1968) and Andalib (1972), respectively, are probably of secondary origin. As pointed out in a previous paper (Mutvei 1967), the conchiolin layer of the connecting rings does not originate from the nacreous layer of the septal neck, but constitutes a separate shell unit which is secreted after the adjacent septal necks have completed their growth. The latter condition is obvious when we consider the growth of the septal neck. It must have projected into a circular invagination of the body proper (text-figs. 6A, B). The epithelium which lined the outer (peripheral) face of this invagination must have secreted the septal neck, whereas in *Nautilus* the septal neck is secreted by the epithelium on the proximal portion of the siphonal cord (Mutvei 1964*a*). Under these circumstances, the conchiolin layer of the connecting ring in prosiphonate ammonoids cannot be a



TEXT-FIG. 6. A. Reconstruction to show the relationship between the soft body and the shell in a prosiphonate ammonoid. B. Detail of fig. A in a higher magnification to show the ontogenetically youngest, prosiphonate septal neck immediately after its formation. C. Similar reconstruction as in fig. B, but at a somewhat later growth stage, showing the formation of the primary conchiolin membrane of the siphonal tube. In all figures the soft body is dotted and the cameral liquid stippled. *e. inv.*, circular invagination of the soft body; *p.m.*, primary conchiolin membrane of the siphonal tube.

continuation of the nacreous layer of the septal neck, as it is in *Nautilus* (cf. Mutvei 1964*a*, 1972). There is, however, a thin conchiolin membrane, here termed the 'primary membrane', which covers the outer face of the septal neck and continues as a thin tube to the succeeding septum, where it is fused to the conchiolin layer covering the dorsal (adapical) face of that septum (Mutvei 1967, and unpublished

scanning electron microscope observations). The primary membrane was probably successively secreted by the epithelium which lined the bottom of the circular invagination of the soft body (*p.m.*, text-fig. 6c). The wall of the siphonal tube in the newly formed chamber was consequently very thin in that it consisted only of the septal neck and the primary membrane (text-fig. 7A). This is in sharp contrast with the condition found in *Nautilus*, where the distal portion of the septal neck and the contiguous connecting ring reach their maximum thickness when only about one-third of the total thickness of the last septum has been attained (Denton and Gilpin-Brown 1966; Mutvei 1972).



TEXT-FIG. 7. A. Reconstruction of an early growth stage in a prosiphonate ammonoid when the wall of the siphonal tube was composed of the septal necks and primary conchiolin membrane only. B. Fully developed wall of the siphonal tube.

Inferred function. The above-mentioned differences in the growth of the wall of the siphonal tube between the retrosiphonate *Nautilus* and the prosiphonate ammonoids have an important functional significance. As demonstrated by Denton and Gilpin-Brown (1966), the new chamber is always completely filled by liquid. This liquid can be pumped osmotically into the siphonal cord through the permeable connecting ring. In *Nautilus*, with its heavy shell, the removal of the liquid from the new chamber

is accomplished at the fastest possible rate, in order to maintain the buoyancy of the animal, because, as the soft body and the shell continue to grow, they increase in weight. However, this cannot take place before the septal neck, and particularly the contiguous, permeable connecting ring have reached their full thickness and strength to withstand the hydrostatic pressure of the sea. Therefore, the wall of the siphonal tube is required to grow faster than the last septum. On the other hand, as just shown, the shell of most ammonoids was considerably more buoyant than that of *Nautilus*, and must consequently have contained much more cameral liquid during life in order to have been in hydrostatic equilibrium with seawater. As a result, there was not the same pressing need for the removal of liquid from the shell chambers and the growth of the connecting rings was retarded (Mutvei 1967). Evidence for the latter condition is that the connecting ring in each chamber was deposited on the inner faces of the two successive septal necks, and consequently secreted by the epithelium of the siphonal cord after the formation of these septal necks and the primary membrane was completed (text-fig. 7B). Both ends of the connecting ring are fused to the adjacent septal necks by a calcareous structure, the auxiliary ridge (text-fig. 7B). The auxiliary ridge is also present in *Nautilus*, but here it only effects the fusion of the distal end of the succeeding connecting ring to the preceding septal neck (Mutvei 1972). As in *Nautilus*, the emptying of cameral liquid in the ammonoids could have taken place only after the connecting rings had reached their full strength. At which stage this has occurred is still obscure. However, the connecting ring of varying numbers of ontogenetically youngest chambers (up to one whorl) are often absent (Trueman 1920; Westermann 1971), which might indicate that there they were not fully developed and were therefore easily destroyed during diagenesis.

Denton and Gilpin-Brown (1966, 1971) have shown that *Sepia* and *Spirula* are capable of regulating the volumes of the liquid in their chambers. This is probably also true for *Nautilus*. For such regulation of the cameral liquid in the ammonoids, a ventral position of the siphonal tube would have been the most advantageous arrangement, and this is supported by the experimental work.

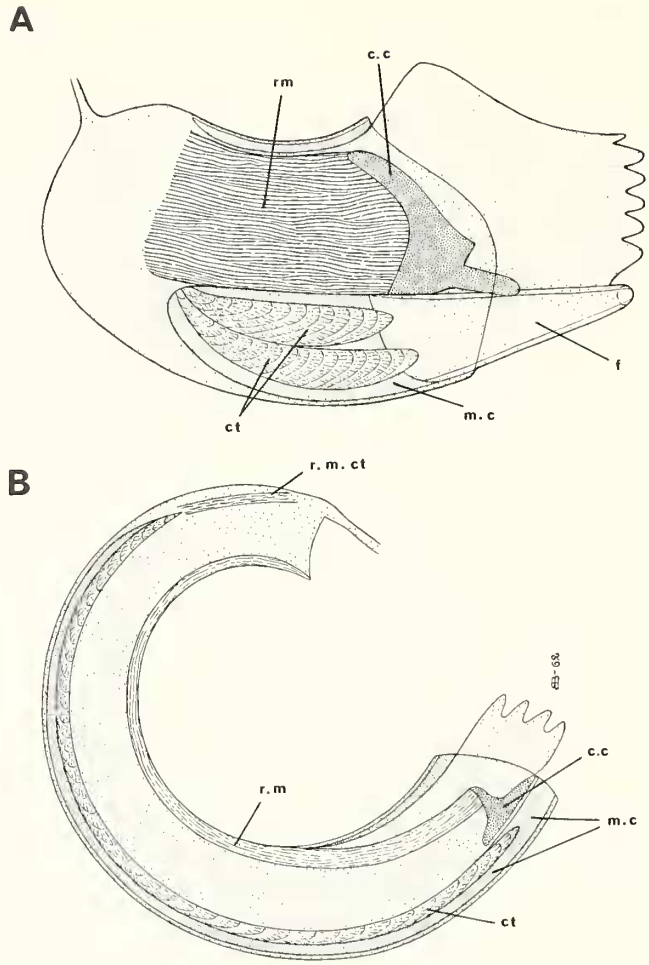
FUNCTIONAL ANATOMY

A comparison between certain shell characters of *Nautilus* and ammonoids allows the following conclusions on the functional anatomy of the latter.

The body chamber of many ammonoids is much longer than that of *Nautilus*. The soft body in these ammonoids must therefore also have been correspondingly longer, and in some forms worm-like (text-figs. 8A and B).

The short-bodied *Nautilus* is well adapted for swimming by jet-propulsion. The mantle fold in *Nautilus* is attached to the shell aperture by the periostracum (Mutvei 1964*a*). This is a general feature for all molluscs which secrete an external shell. Unlike the dibranchiate cephalopods with internal shells, the mantle fold of *Nautilus* therefore contains only a thin muscular layer, the contractions of which are insufficient to drive out the water from the mantle cavity. The ammonoids certainly had the same relationship between the mantle fold and the shell aperture as *Nautilus*.

The swimming mechanism in *Nautilus* has not yet been fully explained. For an



TEXT-FIG. 8. A. Diagrammatic representation of the anatomy in the recent *Nautilus*. B. Reconstruction of the anatomy in an ammonoid. *c.c.*, cephalic cartilage; *ct.*, ctenidia; *f.*, funnel; *m.c.*, mantle cavity; *r.m.*, paired retractor muscles; *r.m.ct.*, an unpaired muscle, probably representing the retractor muscle of ctenidia.

understanding of this mechanism, the following anatomical features must be taken into consideration. The roof above the spacious mantle cavity is formed by a pair of powerful retractor muscles, which originate from the lateral, inner faces of the shell wall (*r.m.*, text-fig. 8A). These muscles extend to the head, where they are rigidly inserted into the cephalic cartilage (*c.c.*, text-fig. 8A). The function of these muscles is not only to attach the soft body to the shell, and withdraw it into the body chamber, as with the columellar muscles in the gastropods. They are also an important part of the swimming equipment of the animal (Griffin 1900; Mutvei 1964*b*).

In order to test the latter assumption, experiments with anaesthetized animals

of the dibranchiates, *Sepia* and *Loligo*, were carried out by H. M. in the summer of 1965 at the Marine Biological Station (ARAGO) at Banyuls-sur-Mer, France. Like other dibranchiate cephalopods, *Sepia* and *Loligo* have a highly muscular mantle, the contractions of which are sufficient to produce a powerful water jet. In order to study the action of the mantle musculature, and the retractor muscles of the head and funnel, the mantle of the anaesthetized animals was cut apart so that the mantle cavity was exposed. On touching the hypobranchial ganglia with a needle, rhythmic, simultaneous contractions of all these muscles take place. In all likelihood, similar simultaneous contractions of the muscles in question occur when the animals swim rapidly, as when escaping from an enemy. These experiments make it reasonable to conclude that when *Nautilus* swims rapidly, the retractor muscles do not remain inactive, but by their contractions create the main force for jet-propulsion. This conclusion is in agreement with the above-mentioned 'roof-position' of these muscles above the mantle cavity. During the muscular contractions, the head of the animal is probably slightly withdrawn into the shell, and the roof of the mantle cavity lowered. This would cause a considerable decrease in the volume of the mantle cavity, as a result of which the water is forced out through the funnel (cf. Griffin 1900; Mutvei 1964*b*). For slow swimming movements, and for respiration, the water is expelled from the mantle cavity by contractions of the funnel (Bidder 1962).

The myo-adhesive scars for the attachment of the paired retractor muscles to the shell wall have been described in several Mesozoic ammonoids by Crick (1898), Jones (1961), and Jordan (1968). These scars have a constant position, in that they are always situated on the dorsal (anatomically anterior) face of the body chamber, irrespective of the shape of the shell. Contrary to this, the scars of the retractor muscles in the fossil 'nautiloids' have a different number and position in different groups (Mutvei 1957, 1964*b*). As in *Nautilus*, the paired retractor muscles of the ammonoids quite probably extended to the head, where they were inserted into the cephalic cartilage (*r.m.*, *c.c.*, text-fig. 8B; see also Mutvei 1964*b*, fig. 8). Owing to their dorsal position, and to the curvature of the soft body, these muscles must have been situated in the dorsalmost portion of the body over most of their extension, close to the dorsal (anatomically anterior) wall of the body chamber (text-fig. 8B). One may therefore conclude that their topographic relationship to the main mantle cavity was different from that in *Nautilus*, and this being so, they could not have formed a roof above this cavity (text-fig. 8B; see also Mutvei 1964*b*, fig. 8E).

To judge from the probable worm-like body shape of many ammonite species, the main mantle cavity in the ammonoids must also have been long and comparatively narrow (*m.c.*, text-fig. 8B), and thus different from the short and broad mantle cavity in *Nautilus* (*m.c.*, text-fig. 8A). The number of the ctenidia is still unknown in the ammonoids, but if they were present, their length would probably have been positively correlated with the length of the mantle cavity. Thus, instead of the rather short ctenidia of *Nautilus* (*ct.*, text-fig. 8A), the ctenidia in the ammonoids may have been long (*ct.*, text-fig. 8B).

Taking into account the shape of the mantle cavity, and the topographic relationship between this cavity and the paired retractor muscles, one may conclude that most ammonoids would have been incapable of efficient swimming by jet-propulsion. Also, the presence of a funnel, necessary for jet-propulsion and steering, is doubtful

for certain ammonoids, which in the adult develop an unpaired, ventral, keel-like projection of the apertural margin. On the other hand, the fossil 'nautiloids' are always provided with an opening for the funnel. The ammonoids were naturally capable of vertical movement in the sea by means of regulation of the volume of the liquid in the shell chambers.

In addition to the paired retractor muscles, the Mesozoic ammonoids also had a small, unpaired muscle in the ventral (anatomically posterior) portion of the body (Jones 1961; Jordan 1968). The myo-adhesive scar for the latter muscle has not yet been found in the Palaeozoic ammonoids (Crick 1898; unpublished observations of H. M.). The extension and function of this unpaired muscle are unknown, but judging from its general position, it may have been homologous with the retractor muscles of the ctenidia in dibranchiate cephalopods (*r.m.ct.*, text-fig. 8B).

POST-MORTAL FATE OF AMMONOID SHELLS

It is now well known that even recently dead *Nautilus* shells do not contain any cameral liquid (Bidder 1962; Denton and Gilpin-Brown 1966). How the post-mortal assimilation and loss of this liquid takes place is still a mystery.

After the death of the animal, the gases deriving from the processes of decomposition of the carcass soon expel water from the body chamber and inflate the decaying soft parts; the dead animal is driven to the surface. The time taken for this is relatively short, usually some few hours. It is therefore clear that at this stage, in the immediate post-mortal phase, the liquid in the chambers remains unaltered in volume. Within a few days at the most, the body parts company with the shell and each passes to its separate fate.

Significant conclusions arising here are that: (1) The ammonoid shell with cameral liquid must have been slightly lighter than water (by analogy with living shell-bearing cephalopods); (2) The density of the body of the ammonoid animal must have been higher than that of water (by analogy with living cephalopods); (3) Irrespective of its structure, the shell and carcass would normally have been forced to the surface shortly after death.

Whether or not the ammonoid lost its cameral liquid during the initial post-mortal phase is a matter for conjecture. There is a reasonable likelihood that at least part of the liquid may have been dissipated during this phase, if the observations made on *Nautilus* have any generality.

There is ample evidence for the vertical embedding of fossil cephalopod shells in sediments (Reyment 1970), and there is little doubt that many shells stranded in semifluid sediment or ooze in their vertical floating positions. In view of the comparative lightness of many ammonoid shells, their relatively high buoyancy, and the necessary requirement of their being lighter than water during life, it is difficult to envisage a situation in which the shell would sink post-mortally without displaying evidence for implosion.

CONCLUDING REMARKS

The structure of the ammonoid siphuncle suggests that it functioned in the same manner as that of living *Nautilus*, albeit with some modification. The development

from retrosiphonate to prosiphonate septal necks tends to be associated with increasing complication of the septa. Secondary simplification of the connecting rings and their retarded growth appears to have been a part of this change. This structural shift could have hardly come about if the ammonoid shell had not evolved in the direction of a buoyancy excess, offset by an increase in the volume of permanent cameral fluid in the living animal. The buoyancy regulation of ammonoid shells probably took place only in those chambers in which the siphuncle had a ventral location, and the cameral liquid, therefore, was in continual contact with the siphuncle. This could be the reason why the majority of the ammonoids had a ventrally located siphuncular tube and why the porous calcareous layers of the siphuncles of many nautiloids, which in living *Nautilus* function in the manner of a 'wick', are absent in ammonoids.

The situation just described is applicable to a large number of ammonoid types. However, extremely evolute shells sometimes have body chambers in excess of one whorl length (Reyment 1973). The effect of this is to offset the uplift of the chambered whorls. It is, we believe, certain that this type of shell must have contained considerably less cameral liquid than other ammonoids, and could therefore have had a specialized mode of life.

Some of our work may cast light on the reason why ammonoids tended to develop complicated cameral sutures with the shell wall. It is no new idea that sutural complications evolved as a means of withstanding water pressure while retaining an optimal thinness of the shell wall. The present study has indicated the strong possibility of the ammonoids having been poorly suited for swimming and more adapted for vertical movement, perhaps connected with a mode of life related to following the diurnal migration of plankton upon which they may have fed. Small size of the prey is indicated by the shape of the jaws (Kaiser and Lehmann 1971). It might therefore be possible that the primary mode of life of the ammonoids involved the need for continual adjustments to a pressure gradient. There is some indirect evidence in support of this interpretation. We know that some ammonites definitely inhabited a shallow-water environment throughout their lives and that they could not have been confronted with the need to adjust to important differences in water pressure. Is this relaxation in the suggested primary mode of life of ammonoids reflected in the suture line?

There are several groups of Cretaceous ammonites that inhabited, permanently, shallow seas. The best known of these is the group of the vascoceratids, the main development of which took place in north-western Africa and the Iberian Peninsula during the Lower Turonian. The vascoceratids have often been said to possess a 'degenerated acanthoceratid suture'. The suture of almost all vascoceratids is indeed greatly simplified in comparison with that of its antecedents and it is not inconceivable that this could have resulted as a genetical response to the pressure-independent mode of life followed by these ammonites in the shallow, epeiric, trans-Saharan sea of the Lower Turonian. This vast inland sea began to develop during the late Cenomanian. At that time it contained the genus *Neolobites*, characterized by a 'pseudogoniatitic' suture. It reached its maximum extension during the Lower Turonian, during which time it stretched from North Africa, across the Saharan region, to Nigeria. The major part of this transcontinental ocean was extremely shallow: its average depth can hardly have exceeded 10 metres, as indicated by the spread of

the sediments in relation to the Upper Cretaceous topography. The shells of most vascoceratid species are more stoutly built than is usual in ammonoids and this would suggest that they were adapted to withstand mechanical damage, resulting from wave action in a shallow environment, rather than the force of water pressure.

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